

Isoetalean Lycopsid Evolution: from the Devonian to the Present

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ABSTRACT.—The evolution of the isoetalean lycopsids spans much of the history of vascular plants, from Late, (or possibly Middle), Devonian to the current day genus *Isoetes*. The best known fossil members of this group are the arborescent lepidodendrids that dominated the Late Carboniferous coal swamps. Simpler unbranched isoetaleans with elongate stems also predated, coexisted with, and postdated the coal swamp trees, extending well into the Mesozoic. Whereas certain synapomorphies such as stigmarian rootlets, bipolar growth and secondary tissues unite the clade, other features characterize smaller subgroups of differing age, growth form and possibly, evolutionary lineage. Although some of these features are well known for plants of given time periods, particularly the Carboniferous, trends in character evolution have never been adequately documented for the group as a whole. A better understanding of such trends throughout the isoetalean fossil record could be valuable in distinguishing evolutionary lineages from convergence. It is interesting that several morphological characters of modern *Isoetes* are present as early as the Triassic: monolete microspores, sunken sporangia and elaborate ligules with glossopodia occur within elongate-stemmed Triassic forms. The dominant plant habit of modern *Isoetes*, a reduced cormose form that lacks appreciable stem elongation, originated at least by the Jurassic and typifies late Mesozoic and Cenozoic isoetaleans.

The lycopsids have always held a particular fascination for paleobotanists and neontologists alike because of their diverse morphologies, long stratigraphic record and their phylogenetic position as the outgroup to the rest of the vascular plants (Gifford and Foster, 1989; Kenrick and Crane, 1997). Whereas most lycopsids are similar to other pteridophytes in their growth habit and life history, isoetalean plants are characterized by distinctive morphological innovations, including secondarily derived bipolar growth, secondary cortical (and possibly vascular) tissues and arborescence. This group is generally thought to make its first appearance in the Late Devonian, or perhaps earlier, and reach its greatest diversity and ecological importance in the Late Carboniferous. Isoetaleans continue into the Early Mesozoic, where they are represented worldwide by numerous species of *Pleuromeia* Corda, *Annalepis* Fliche and several other forms. In the Jurassic, plants quite similar to modern *Isoetes* L. first appear. They continue to diversify throughout the Cretaceous and Tertiary and up to the present day.

The best known members of the Isoetales are the arborescent lepidodendrids, a group that dominated the Late Carboniferous (= Middle-Upper Pennsylvanian) coal swamp of Euramerica. These heterosporous trees had multi-branched crowns of varying forms, long microphyllous leaves attached to characteristic diamond- or hexagonal-shaped leaf cushions, thick secondary cortical tissues, well developed stigmarian rooting systems and often monosporangiate cones with reduced numbers of megaspores and specialized

modifications for dispersal (Phillips, 1979; Bateman *et al.*, 1992; Phillips and DiMichele, 1992). Most of the arborescent forms became extinct by the Late Carboniferous of Euramerica concomitant with the loss of the most extensive coal swamp habitats (Bateman, *et al.*, 1992; Stewart and Rothwell, 1993). However, growing alongside the Middle Pennsylvanian tree lycopsids and surviving after them into the Late Carboniferous (Upper Pennsylvanian) were smaller (1–2 m tall), unbranched or rarely branched isoetaleans such as *Chaloneria* Pigg & Rothwell and *Sporangiostrobus* Bode (Pigg and Rothwell, 1979, 1983a, 1983b, 1985; Wagner, 1989). It is now known that isoetaleans with this elongate, unbranched growth habit originated by the Late Devonian (e.g., *Clevelandodendron* Chitaley & Pigg, Chitaley and Pigg, 1996) and were widespread throughout the Triassic where they belonged to at least two broad groups, *Pleuromeia*-like and *Annalepis*-like forms and their relatives (Pigg, 1992; Grauvogel-Stamm and Lugardon, 2001). Today the order Isoetales is represented by a single genus, *Isoetes*, which remains one of the most unusual living pteridophytes and retains many morphological, anatomical and developmental features that reflect its origins (e.g., Stewart, 1947; Gifford and Foster, 1989; Bateman, *et al.*, 1992; Pigg, 1992).

Recent studies have provided new information about the origin, evolution and diversity of the Isoetales. In this contribution, four phases of evolution in isoetalean lycopsids are addressed: (1) presumed Devonian origins of the Isoetales; (2) their maximum diversity in the Late Carboniferous, (3) Mesozoic plants with the growth habit of modern *Isoetes*, (4) new occurrences of Cretaceous and Tertiary forms. Lastly, problems of relating fossil taxa to extant *Isoetes* are addressed and suggestions are outlined for a better understanding of the isoetalean lineage through time.

ORIGIN OF ISOETALEAN LYCOPSIDS

Historically, the Isoetales, the rhizomorphic heterosporous lycopsids, have been assigned to a variety of orders including the Lepidodendrales, Pleuromeiales, Isoetales and some forms occasionally to Protolpidodendrales (Chaloner, 1967; Pigg and Rothwell, 1983b; DiMichele and Bateman, 1996; Kenrick and Crane, 1997), and even, probably mistakenly, the Selaginellales (see Rothwell and Erwin, 1985). In this paper I follow DiMichele and Bateman (1996), who recognize the entire group within the order Isoetales, based on a suite of synapomorphies including bipolar growth, secondary tissue production, and stigmarian rootlet formation.

Whereas much is known about both vegetative and reproductive structure of fossil isoetaleans, particular attention has been given to the basal parts, or rhizomorphs of the plants, especially the size and shape of their lateral lobes or horns. A great deal of diversity has been documented for these rhizomorphic features which vary from elongate, dichotomizing rooting systems of *Stigmaria* Brongniart to smaller bilaterally symmetrical lobed or rounded forms (e.g., *Pleuromeia*), to radial unlobed forms (e.g., *Paurodendron* Fry). All of these rhizomorphic forms can be homologized (Rothwell and Erwin, 1985; Grauvo-

gel-Stamm and Lugardon, 2001). It is now clear that the shape of the rhizomorph, or even its symmetry, is not nearly as significant as its production of stigmarian appendages or "rootlets" with their characteristic anatomy and the likelihood of their secondary derivation from an aboveground shoot system. This fascination with the basal portions of the plants has been particularly centered around the stigmarian rooting system and its ubiquity among Late Carboniferous coal swamp lepidodendrids. There has been interest for some time in finding evidence for the origin of *Stigmaria*, with the underlying assumption that this would lead toward understanding the origin of the isoetalean clade as a whole. Devonian and Early Carboniferous plants that obtained tree stature and/or those which produced rhizomorphic plant bases have been sought as the ancestors of lepidodendrids. The best known candidates have been the enigmatic "Naples tree" *Lepidosigillaria whitei* Kräusel & Weyland from New York State and *Cyclostigma kiltorkense* Haughton, from Late Devonian strata in several areas of Ireland and Bear Island in the Arctic, and China.

Lepidosigillaria whitei Kräusel & Weyland, a large stem with a plant base that appears rounded and lacking a stigmarian rooting system, occurs in the Late Devonian of New York State (Grierson and Banks, 1963). The original specimen was over 5 m tall and demonstrated that well developed, arborescent lycopsids had clearly evolved by the Late Devonian (White, 1907; Kräusel and Weyland, 1949; Grierson and Banks, 1963; Chaloner, 1967). Because of lateral compression during fossilization, the exact nature of the plant base of *Lepidosigillaria* is unknown. However, there is some increased thickening of basal cortical tissues, suggesting secondary tissues were produced. Several distinctive decortication layers are recognized on the stem surface, and small (less than 3 cm long), very narrowly attached leaves occur at higher levels. Although *Lepidosigillaria* has been described as having rootlets attached to the plant base (White, 1907), preservation is poor and their presence cannot be verified (Gensel and Berry, 2001).

A second Late Devonian lycopsid, *Cyclostigma kiltorkense* Haughton, has also been difficult to interpret. This plant was originally described from the Upper Devonian of Ireland, and later found in Bear Island, in the Arctic, and China (Johnson, 1913; Chaloner, 1967, 1968; Schweitzer, 1969; Cai and Wu, 1994). *Cyclostigma* is described as a large, heterosporous plant with characteristic rounded leaf scars (Chaloner, 1967) and is reported to have a bilobed plant base (Johnson, 1913). Specimens showing plant bases may be known (Chaloner, pers. comm. 1999) but they have never been clearly illustrated and have yet to be studied in detail. It also remains unclear whether all plant remains assigned to this genus represent the same plants. Clearly, reinvestigation of this problematic genus is in order.

Despite the currently limited information about *Lepidosigillaria* and *Cyclostigma*, their occurrences have established the presence of large isoetalean plants at least as early as the Late Devonian. In recent years additional Late Devonian and older, Middle Devonian lycopsids with a presumed relationship to the Isoetales have been reported. The Middle Devonian *Longostachys latis-*



FIG. 1. Line diagram of the rootstock of *Longostachys latisporophyllus*. Redrawn from Cai, Chongyang, and Lizhu Chen, 1996.

porophyllus Zhu, Hu & Feng *emend.* Cai & Chen was described from Givetian strata of southern China (Cai and Chen, 1996; Gensel and Berry, 2001). *Longostachys* is reconstructed as a small, branching heterosporous lycopsid tree that was up to 1.5 m tall with a stem 3.5 cm wide and a plant base that had a three-dimensional funnel-like structure with thick, rootlike appendages (Fig. 1). Because of its bipolar growth and centralized rooting system, this Middle Devonian plant may have some significance to isoetalean origins. The rooting structure of *Longostachys* bears some resemblance to stigmarian appendages, however it apparently lacks the dichotomizing stigmarian axes and characteristic stigmarian rootlet scars. Given the plant's Middle Devonian age it may be that these rooting organs are modified branching axes that cannot be clearly defined as stem or root, and may be more comparable to the H & K branching characteristic of zosterophylls (Gensel and Berry, 2001). However, well-defined leaves and strobili are produced by *Longostachys*, indicating that true leaves and stems had evolved by then. Whatever their exact homologies, the rooting structures of *Longostachys* suggest a potential intermediate step in the evolution of bipolar growth and the origin of stigmarian rooting systems in isoetaleans.

Additional Late Devonian isoetaleans have been discovered in Pennsylvania and Ohio. A flora from Red Hill, Pennsylvania contains cormose lycopsid plant bases (Cressler, 1998, 1999; Scheckler, *et al.*, 1999). Five specimens with attached rootlets have been recovered from oxbow lake facies of this fluvial deposit. One specimen has a stem width of 10 cm and a flared base of 12 cm, and with two lobes visible and is estimated to have four lobes. A second specimen is approximately 2 cm wide with a flared base. Roots are borne in orthostichies, with largest roots adjacent to one another. Associated, usually un-

branched, stems have various decortication patterns including *Knorria* Sternberg, *Helenia* Zalesky and *Cyclostigma*, as well as *Lepidodendropsis* Lutz-like pseudowhorls. Reproductive structures are not yet known (Walter L. Cressler, University of Pennsylvania, pers. comm. 1999). The Elkins, West Virginia locality that provided the earliest seed plant, *Elkinsia*, is of comparable age to Red Hill, and also contains lycopsid stems but plant bases are not yet known from Elkins (Gar W. Rothwell, Ohio University, pers. comm. 1999).

Another recently recognized Late Devonian plant with an elongate isoetalean plant habit is *Clevelandodendron ohioensis* Chitaley & Pigg from the Cleveland Shale (Chitaley and Pigg, 1996). The genus is based on a single specimen which represents the entire plant. *Clevelandodendron* is an unbranched, slender plant with a compact terminal bisporangiate cone at the apical end and a partially preserved plant base proximally. The specimen is 125 cm long from base to apex and 2 cm wide for most of its length. Although details of the plant base are obscure, it appears to bear several thick appendages that taper distally and an elongate stigmarian root system is lacking. The terminal bisporangiate cone contains trilete megaspores that are laevigate (smooth) and trilete microspores that conform to either *Calamospora* Schopf, Wilson & Bentall or *Punctatisporites* (Ibrahim) Potonié & Krempf. Ligules are not known. *Clevelandodendron* is of particular significance because it demonstrates that elongate, slender isoetalean lycopsids with an unbranched plant habit, more common in later isoetalean forms, were present as early as the Late Devonian.

Plant remains with similarities to *Clevelandodendron* are also known in younger, Lower Carboniferous strata at several localities in eastern North America, France and Ireland. For example, anatomically preserved stems of similar dimensions are present in Lower Carboniferous localities in France (Brigitte Meyer-Berthaud, Université Montpellier, pers. comm. 1996) and additional permineralized stems showing cortical and stelar features transitional between the traditional *Protolepidodendrales* and *Lepidodendrales* occur at a variety of localities in North America, (e.g., Andrews, Read and Mamay, 1971; Cichan and Beck, 1987; Roy and Matten, 1989), Ireland (Matten, 1989; Roy and Matten, 1989), Scotland (Beck, 1958), and France (Meyer-Berthaud, 1984). Several bisporangiate cones with spore types similar to those of *Clevelandodendron* have been described from Upper Devonian and Lower Carboniferous strata of France and eastern North America (Arnold, 1933, 1935, 1939; Mathews, 1940; Meyer-Berthaud, 1984). These bisporangiate cones with laevigate (smooth) megaspores are unlike the stratigraphically younger bisporangiate cones of *Flemingites* Carruthers. The genus *Flemingites* bears *Lycospora* Schopf, Wilson & Bentall microspores with an equatorial flange, and *Lagenicula* (Bennie & Kidston) Potonié & Krempf or *Lageniosporites* Potonié & Krempf megaspores with an apical spore extension called a gula (Brack-Hanes and Thomas, 1983). Thus, not all Paleozoic bisporangiate lycopsid cones can be assigned to *Flemingites* (Chitaley and Pigg, 1996). Species of *Flemingites* are thought to have been borne by small lepidodendrid trees such as *Paralycopodites brevifolius* (Williamson) DiMichele (e.g., Brack, 1970; DiMichele,

1980). Thus there may be at least two lineages of Paleozoic lycopsids that produced bisporangiate cones: those related to *Clevelandodendron* and those bearing *Flemingites* cones.

One interesting Lower Carboniferous plant of isoetalean affinities is the *Protostigmaria/Lepidodendropsis* plant. *Protostigmaria* Jennings plant bases are reported to have had up to 13 lobes and a maximum width of 32 cm. This multilobed rooting structure was initially described by Jennings (1975) and later studied by Jennings, Karris and Rothwell (1983). These authors suggested that *Protostigmaria* grew like *Isoetes*, with new lobes being produced by forking at the ends of furrows. The presumed above-ground parts of *Protostigmaria*, assignable to *Lepidodendropsis* Lutz are found both at the same and at several additional nearby sites in the Mississippian Price Formation of Virginia (Patricia G. Gensel, personal communication, 1999). Above-ground parts of *Lepidodendropsis* suggest the plant was a tree that branched dichotomously and may have had determinate growth. It was apparently eligulate but heterosporous and had linear leaves. Middle Devonian fossils assigned to *Lepidodendropsis* may represent a mix of several different plants that may not be equivalent to this Lower Carboniferous plant. Study and correlation of *Protostigmaria* plant bases and vegetative stems at several decortication layers of *Lepidodendropsis* and reproductive remains from the same localities will provide the opportunity to reconstruct this interesting Lower Carboniferous lycopsid (Gensel and Pigg, in progress).

LATE CARBONIFEROUS DIVERSITY

During the Late Carboniferous, diversity and ecological importance of isoetalean plants reached their maximum. Arborescent lepidodendrids are extensively well known as both permineralizations in coal ball floras, and as coalified compressions. Whole plant reconstructions, reproductive biology and paleoecological aspects of these plants have been reviewed elsewhere (e.g., Phillips, 1979; Bateman, et al., 1992).

The extensive information available about Carboniferous lepidodendrids has allowed for the whole plant reconstruction of several species including the bisporangiate *Paralycopodites*, and larger monosporangiate trees with specialized dispersal units that have been modified presumably for water dispersal (Phillips, 1979). These include *Diaphorodendron* DiMichele and *Synchysidendron* DiMichele & Bateman, genera with two different crown branching forms that both produce *Achlamydocarpon varius* (Baxter) Taylor & Brack-Hanes, a megasporangium with a specialized, thickened wall surrounding a single functional megaspore (DiMichele and Bateman, 1992). Another tree lycopsid, *Lepidophloios* Sternberg, produces *Lepidocarpon* Scott, a cone that breaks up into individual megasporophyll units that contain the megasporangium with a single functional megaspore surrounded by an elongate and elaborated sporophyll (Phillips and DiMichele, 1992). Another tree form, *Sigillaria* Brongniart, bore monosporangiate cones on lateral cauline peduncles. Permineralized megasporangiate cones of *Sigillaria*, *Mazocarpon* (Scott) Benson produced 4–8 large

megaspores that are found each associated with a portion of sporangial wall and a pad of sterile tissue (Schopf, 1941; Pigg, 1983; Phillips and DiMichele, 1992). Parallels of these specialized forms with the seed habit have been commonly made (e.g., Phillips, 1979; Thomas, 1981).

We now know that in addition to the large arborescent lepidodendrids, which themselves were quite diverse, isoetaleans had a variety of other plant habits. These included the small scrambling "pseudoherbs" *Oxroadia* Alvin and *Paurodendron* Fry, as well as the unbranched monopodial plants *Chaloneria* Pigg & Rothwell and *Sporangiostrobus* Bode. *Oxroadia*, a plant of Lower Carboniferous age, is known from a number of localities in England and Scotland (Bateman, 1992), while *Paurodendron* has been described from Middle and Late Pennsylvanian coal ball floras of eastern and midcontinent North America (Rothwell and Erwin, 1985). Comparative developmental studies of apical and lateral growth of rhizomorphs in *Paurodendron*, *Stigmara*, *Nathorstiana* Richter and modern *Isoetes* have been instrumental in understanding homologies across the isoetalean clade (Karrfalt, 1984; Rothwell, 1984; Rothwell and Erwin, 1985; Rothwell and Pryor, 1991).

The genus *Chaloneria* is reconstructed as a whole plant based on permineralized stems, fertile areas with *in situ* spores, decortication surfaces, and megagametophytes (Pigg and Rothwell, 1979, 1983a, 1983b, 1985). In contrast to the well known lepidodendrids, *Chaloneria* was more like its Devonian relative, *Clevelandodendron*, in having an unbranched, elongate stem. Instead of compact cones *Chaloneria* exhibits a less well differentiated fertile area that occurs either apically with alternating mega- and microsporangiate zones (*C. cormosa* Pigg & Rothwell) or alternating vegetative and fertile zones (*C. periodica* Pigg & Rothwell; DiMichele, Mahaffy and Phillips, 1979; Pigg and Rothwell, 1983a, 1983b). These and presumably related forms share the megaspore type *Valvisisporites* Ibrahim (Gastaldo, 1981) and microspores of *Endosporites* Wilson & Coe (e.g., Brack and Taylor, 1972; Hanes, 1975).

Compressed lycopsid reproductive structures bearing the same spore types as *Chaloneria* are given the name *Polysporia* Newberry (Chaloner, 1958; Dräbek, 1976a, 1976b; DiMichele, *et al.* 1979; Pigg and Rothwell, 1983b). Previous reports of *Polysporia* were from incompletely preserved specimens, and it was difficult to tell whether these structures were compact cones or fertile areas such as those of *Chaloneria*. A recent study of well-preserved, complete cones of a new species of *Polysporia* from France, *P. doubingeri* Grauvogel-Stamm & Langiaux shows that *Polysporia* was at least sometimes a compact cone rather than an undifferentiated fertile area (Grauvogel-Stamm and Langiaux, 1995). This study brings to question whether all plants that produced these characteristic spore types, well known from Middle Pennsylvanian coals (Pigg, 1992), had the same type of growth habit (Pigg and Rothwell, 1983b, Grauvogel-Stamm and Langiaux, 1995).

Sporangiostrobus Bode is known from coal ball floras of the Middle Pennsylvanian of Kansas and compressed floras from the Stephanian (= Upper Pennsylvanian) of Spain (Pigg and Rothwell, 1983b; Wagner, 1989 and references cited therein). This plant parallels the *Chaloneria/Polysporia* plants in

stem anatomy, size, unbranched to rarely branched habit and presence of fertile areas rather than compact cones. These plants grew in nearly monotypic stands, a situation also common in later pleuromeian forms (e.g., Retallack, 1975; Fuchs *et al.*, 1991; Pigg, personal observation, 1991). In contrast to *Chaloneria/Polysporia* plants, *Sporangiostrobus* bore the highly variable *Densosporites* (Loose) Schopf, Wilson & Bentall microspores, characterized by a prominent equatorial ridge, the cingulum, and *Zonalesporites* (Bartlett) Leisman megaspores. Whereas Pigg and Rothwell (1983b) suggested that *Sporangiostrobus* may be assignable to the same family as *Chaloneria*, the Chaloneriaceae, similarities of the two groups may be more the result of convergence in growth habit. Several other Carboniferous forms which, for various reasons, have been allied with the isoetales are reviewed by Pigg (1992).

ORIGIN OF MODERN *ISOETES* PLANT HABIT AND MORPHOLOGICAL FEATURES

As the Paleozoic ended and most of the large, specialized lepidodendrid plants died out, a variety of several smaller, elongate, unbranched forms remained. These are represented in the Mesozoic by the genera *Pleuromeia* Corda, *Annalepis* Fliche and several other diverse forms (Pigg, 1992; Skog and Hill, 1992; Retallack, 1997; Grauvogel-Stamm and Lugardon, 2001). Around a dozen species of *Pleuromeia* have been named from numerous localities throughout the world including Germany, Russia, China, Japan and Australia (Pigg, 1992). Some pleuromeian genera, such as *Cylomeia* (White, 1981) and *Lycomeia* (Dobruskina, 1985) have been proposed on basis of the geographic occurrence, morphology and mono- vs bisporangiate nature of plants. However, whereas numerous species of *Pleuromeia* have been described and some are well known (e.g., Grauvogel-Stamm, 1993), the overall diversity and interrelationships of these taxa remain obscure.

In addition to pleuromeians there are a suite of Triassic plants assigned to *Annalepis* and related taxa which have been described by Grauvogel-Stamm and colleagues (Grauvogel-Stamm and Düringer, 1983; Grauvogel-Stamm and Lugardon, 2001). This latter group appears distinct from pleuromeians on the basis of a number of features including sporophyll morphology and spore characters. In some features *Annalepis* may resemble some later isoetales of Cretaceous-Tertiary ages (Grauvogel-Stamm and Lugardon, 2001).

A third source of Triassic lycopsids is the discovery of several permineralized forms. These include *Takhtajanodoxa* Snigirevskaya from Russia (Snigirevskaya, 1980a, 1980b), forms attributed to *Pleuromeia*, also from Russia (Snigirevskaya and Srebrodelskaya, 1986) and the more recently reported permineralized lycopsids from the Lower Triassic of Australia (Cantrill and Webb, 1998). The affinities of permineralized Triassic forms and their relationships to the more widely known compressed remains have not been fully resolved.

In the early 1980's Snigirevskaya described the permineralized Triassic plant *Takhtajanodoxa* from Russia (Snigirevskaya 1980a, 1980b). This plant has stem, leaf and megaspore anatomy similar to *Chaloneria* and other Pennsylvanian lycopsids. What is surprising, however, is the presence of elaborately

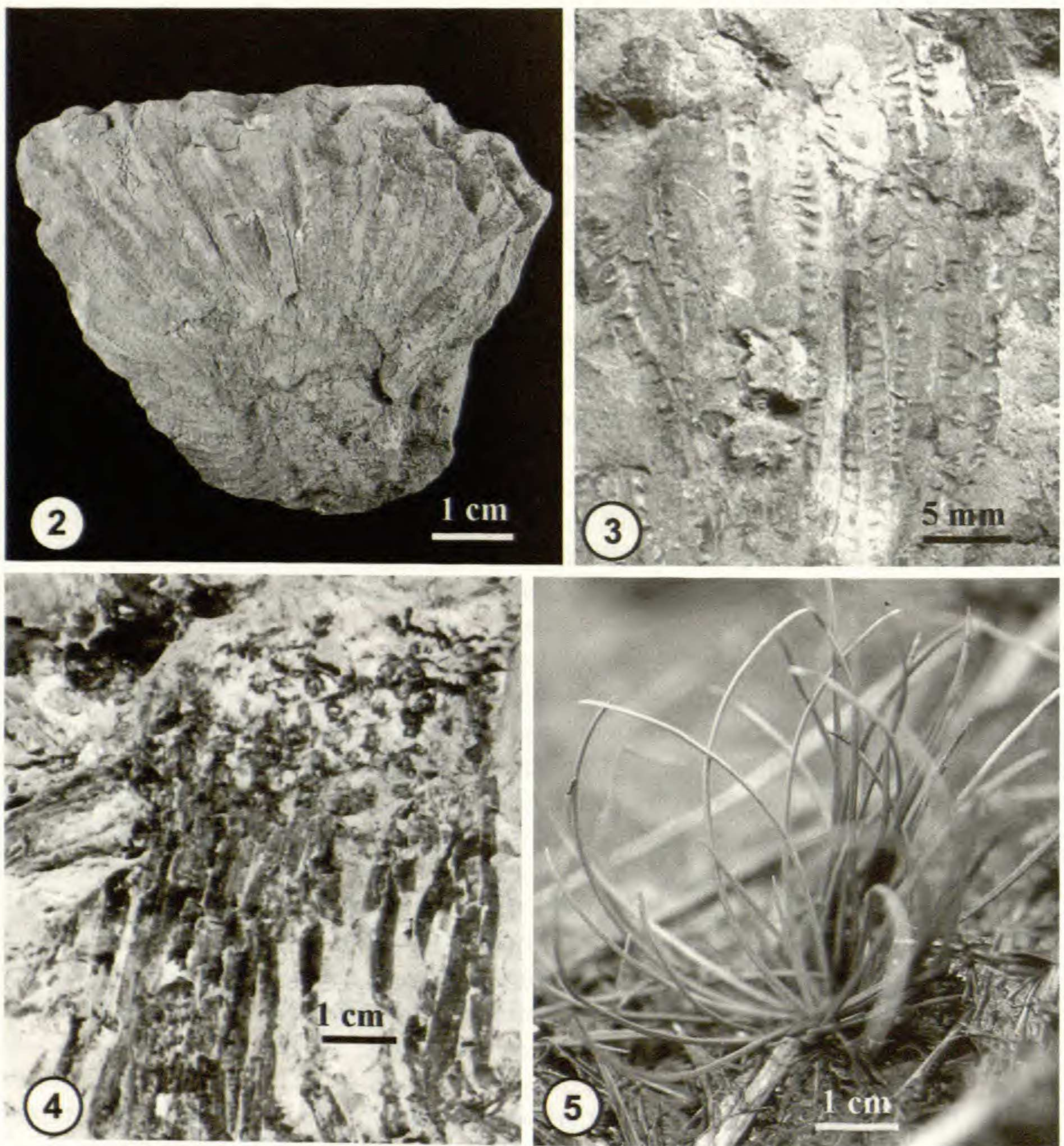
shaped ligules with curving basal extensions of the glossopodium (Snigirevskaya, 1980a, 1980b; Pigg, 1992). This type of ligular structure is lacking in Paleozoic permineralized lycopsids but present in extant *Isoetes* (Gifford and Foster, 1989). Permineralized stems described as *Pleuromeia* were also characterized from Russian Lower Triassic strata (Snigirevskaya and Srebrodel'skaya, 1986). These specimens show small, protostelic stems lacking secondary tissues with mesarch leaf traces, and fimbriate metaxylem tracheids with scalariform and reticulate wall thickening patterns. More recently, permineralized forms have been described from the Lower Triassic Bowen Basin of eastern Australia by Cantrill and Webb (1998). These authors describe a suite of disarticulated lycopsid plant organs that include one bisporangiate and one monosporangiate cone type, two types of stems, one with prominent aerenchyma in the cortex, and one type of rooting structure that bears stigmarian-like rootlets. From the presently known information, at least two types of lycopsids thus appear to be present in these remains. As with late Carboniferous coal ball lycopsids, for the first time the exciting potential exists for "whole-plant" reconstructions of Lower Triassic isoetaleans, based on the co-occurrence, anatomical similarity and organic interconnections between these separate plant organs.

It is during the Mesozoic that we see the origin of a number of morphological features present in modern-day *Isoetes*. These features include: 1) a change in microspores from trilete to monolet suture (and probably also change in tetrad arrangement); 2) sporangia that are sunken into the adaxial surface of the sporophyll; 3) an elaboration of the basal portion of the ligule into a glossopodium; 4) the origin of a velum and/or a labium, covering the proximal, distal, or entire upper surface of a sporangium.

All of these features can be seen among various Triassic-aged plants. Microsporophylls of *Annalepis* are characterized by monolet microspores of the *Aratrisporites* (Leschik) Playford & Dettman type (Grauvogel-Stamm and Lugardon, 2001). Sporangia are notably sunken into the sporophyll surface in several species of *Pleuromeia* such as *P. rossica* Neuburg and *P. longicaulis* (Burgess) Retallack (Neuburg, 1960, 1961; Retallack, 1975). Ligules with an extended basal glossopodium much like that present in many extant species of *Isoetes* occur in the permineralized Triassic Russian plant *Takhtajanodoxa* (Snigirevskaya 1980a, 1980b; Pigg, 1992).

Whereas it appears that no single currently known Triassic isoetalean taxon possesses all of these features, all are found within various representatives of Triassic lycopsids. As the Triassic and later Cenozoic lycopsids are better documented, it will be possible to better understand character evolution in the various lineages of Triassic lycopsids (Grauvogel-Stamm and Lugardon, 2001). This suggests the Triassic was a time of important radiation and change in several key morphological characters prior to the appearance of the extant, reduced *Isoetes* forms.

The origin of the modern *Isoetes* plant habit with a nonelongated stem was previously thought to occur in the Triassic (Pigg, 1992). However, evidence for this type of plant habit is scant, as the best documented Triassic *Isoetes*-like



FIGS. 2–5. Tertiary and extant isoetalean lycopsids. Fig. 2. cf. *Isoetites* from Dennison Gap, Wyoming. Florida Museum of Natural History. UF 18120–12604. Fig. 3. Detail of specimen from Dennison Gap, showing square air channel pattern on sporophyll surfaces. Florida Museum of Natural History. UF 18120–12604. Fig. 4. Joffre Bridge isoetalean plant. University of Alberta 539–421. Fig. 5. *Isoetes tegetiformans* habit shot.

plant, *I. gramineoides* (Ward) Bock, originally considered a grass, has been reidentified as a fern petiole (Bock, 1962; Skog and Hill, 1992). Another well known form, *I. circularis* from the Triassic of eastern North America, more closely resembles the genus *Annalepis* in sporophyll features, and its plant corms, whether elongate or reduced, have not been well documented (Grauvogel-Stamm and Lugardon, 2001). Recently, several authors have proposed additional *Isoetes* species in the Triassic (e.g., Wang, 1991; Retallack, 1997).

Although it is clear that all of these forms are isoetalean plants, none show undisputed evidence of a non-elongating stem such as is usually characteristic of modern *Isoetes*. They should certainly be included within the Isoetales, based on their particular morphological features, yet I am reluctant to accept them as belonging to the modern genus.

The earliest strong evidence of the modern plant habit is that seen in the Jurassic *Isoetites rolandii* Ash & Pigg from western North America (Ash and Pigg, 1991). Concomitant with this change in plant habit is the loss of vegetative leaves: modern *Isoetes* and its younger fossil relatives typically produce only fertile leaves, thereby minimizing the vegetative phase of its life history.

CRETACEOUS AND TERTIARY—SOME NEW OCCURRENCES

Over a dozen *Isoetes*-like plants have been described in Cretaceous and Tertiary strata (see Pigg, 1992, and Skog and Hill, 1992 for review). Several newly recognized forms have been recently described. One unusual example is *Monilitheca* Krassilov & Makulbekov described from the Upper Cretaceous of Mongolia by Krassilov and Makulbekov (1996). The genus consists of fragmentary linear megasporophylls up to 18 mm long and 1 mm wide that bear within the sporangium, a single row of megaspore tetrads. These tetrads are borne along almost the entire length of the megasporophyll, which has a short sterile tip. Megaspores are trilete, and reticulate.

Isoetalean plants described from the Lower Cretaceous of Tunisia were named *Isoetites daharensis* Barale (1999). These fossils are represented by corms 10 cm long \times 6 cm wide with attached sporophylls and roots. Sporophylls are ligulate and bear sporangia containing trilete megaspores 480 μ m in diameter. Isoetalean plants have also been recognized in the lower Cretaceous of Brazil, in the Santana Formation (Dilcher *et al.*, 2000). In this flora, *Isoetes*-like plants are represented by clusters of sporophylls that occur along with ferns, conifers, angiosperms, and abundant gnetalean remains.

In the Tertiary, plants from the Paleocene Joffre Bridge locality in central Alberta, Canada originally identified by Hoffman as lilean monocots are clearly isoetalean (Hoffman, 1995, Plate 14, figs. 101, 102). The specimen is a plant base approximately 5.5 cm long and around 3 cm high with a crown of elongate leaves at the top of the specimen. At the base dense, helically arranged, rounded stigmarian rooting scars are present, a feature diagnostic for the isoetalean clade (Fig. 4). Around twenty stigmarian rootlets, each measuring 3 mm wide and over 7 cm long, are found in attachment to the plant base.

Additional isoetalean specimens are known from the Lower Eocene Dennison Gap locality of the Wasatch Formation near Sweetwater, Wyoming, where they occur with platycaryoid foliage, fructifications and *Azolla* (Steven R. Manchester, Florida Museum of Natural History, written communication, 1992; Fig. 2, 3). These specimens are probably assignable to either *I. horridus* or *I. serratus* of Brown, depending on details of the leaf margin that are not readily visible, and show the characteristic air channels that are often found in *Isoetites* leaves (Fig. 3; Brown 1939, 1958, 1962).

CONCLUSIONS AND SUGGESTIONS FOR FURTHER RESEARCH

In recent years, valuable new types of information have appeared that promise to help clarify long-held questions about the evolution of the isoetalean clade. Notable are newly discovered 1) Middle Devonian forms from China that may have some bearing on the origins of this order, 2) permineralized Triassic fossils that provide a missing "middle" to our knowledge of anatomical features between Paleozoic forms and extant *Isoetes*, and 3) Cretaceous and Tertiary forms that document additional diversity of the group. Phylogenetic analyses of anatomically preserved Carboniferous forms have been successful in delimiting interrelationships among the most complex isoetaleans which have been documented as "whole plants" and are understood ecologically (e.g., Bateman *et al.*, 1992; Phillips and DiMichele, 1992). However, to date it has not been possible to extend these types of studies beyond that stratigraphic range because of the limitations of preservation and difficulty of homologies.

Whereas researchers studying Devonian, Pennsylvanian or Triassic aged fossils or extant *Isoetes* have made partial comparisons, homologies of characters through geological time have been more difficult. Part of the problem has been the use of terminology developed for one group of lycopsids for a different group. In some cases, terms and concepts have had to be "stretched" to accommodate real differences between isoetalean lycopsids of different ages. What is needed is an analysis of overall diversity within given characters, such as sporophyll morphology, without terminology imposed *a priori*.

Lastly, with all of the work done on fossil and extant isoetaleans to date, the question of how to define the modern genus *Isoetes* in relation to its fossil relatives has never been resolved. In the present contribution I have referred to the extant *Isoetes* plant habit as having a reduced, non-elongating stem. However, there is considerable morphological variation in extant species. In addition to "typical" plants there are forms with branching axes such as *I. andicola* (formerly *Stylites* Amstutz), and the unusual rhizomatous mat-forming *I. tegetiformans* Rury (Fig. 5). Some species of *Isoetes* have even been observed to have small rhizomorphic structures (W. Carl Taylor, pers. comm. 1999).

However, despite this diversity, it is well known among neontologists that morphology has been of little value in understanding speciation in *Isoetes* because of the high degree of homoplasy and convergence to habitat (e.g., Taylor and Hickey, 1992). Despite numerous discussions, it is still unclear what is basal in the group based on morphology because of the strong imprint of ecological influence. Molecular studies that clarify extant species relationships may help us resolve this problem and offer clues to the relationships of the extant and relatively recent fossil isoetaleans. Further developmental studies of *Isoetes* may also aid in a better understanding of homologies. Nevertheless, the fossil record still promises to resolve much more about diversity and evolution within this interesting group throughout its long evolutionary history.

ACKNOWLEDGEMENTS

I thank W. Carl Taylor, N. Wickstrum, and Lea Grauvogel-Stamm for inviting my contribution to this symposium and the American Fern Society for travel funds to the symposium; Charlotte M. Christy, Walter L. Cressler, Melanie L. DeVore, Else Marie Friis, Patricia G. Gensel, Judith E. Gordon, David M. Jarzen, Steven R. Manchester and Ruth A. Stockey for access to material and field localities and assistance; Melanie L. DeVore, Patricia G. Gensel, Lea Grauvogel-Stamm, R. James Hickey, Gar W. Rothwell and Wesley C. Wehr for their comments on the manuscript; Stefanie M. Ickert-Bond for technical assistance, and Gar W. Rothwell and W. Carl Taylor for numerous discussions on isoetalean lycopsids. This research was supported in part by NSF EAR-9980388.

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